

Diplochory: are two seed dispersers better than one?

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Diplochory is seed dispersal by a sequence of two or more steps or phases, each involving a different dispersal agent. Here, we describe five forms of diplochory and derive general characteristics of each phase of seed dispersal. The first and second phases of diplochory offer different benefits to plants. Phase one dispersal often results in escape from density-dependent seed and seedling mortality near the parent plant and can result in the colonization of habitat patches far from the parent. Phase two dispersal often moves seeds to discrete and predictable microsites, where the probability of seedling establishment is disproportionately high (i.e. directed dispersal). Diplochory appears to have evolved because combining two means of seed dispersal can increase the benefits of seed dispersal whilst reducing the likelihood of seed mortality.

The dispersal of seeds and other plant propagules is often a complex, multi-step process. Some complex forms of seed dispersal (diplochory) comprise two phases, with distinctly different dispersal mechanisms (Figure 1, Box 1). Phase one is the initial mode of seed movement away from the parent plant, whereas phase two is the subsequent movement by another mechanism. We draw a distinction between diplochory and other forms of dispersal that

Box 1. The big picture

- Seeds of many plants are dispersed in two or more 'phases', with a different type of dispersal agent involved in each.
- For such plants, phase one dispersal moves seeds away from the influence of the parent plant (reducing potential competition between seedling and parent) and reduces losses to seed predators by distributing seeds widely.
- Phase two often moves seeds to safe sites (e.g. below ground), where they are relatively protected from seed predators, and the chance of successful germination and seedling establishment are enhanced.
- The combination of two dispersal mechanisms often provides greater benefits to seeds than do most single means of dispersal.
- Diplochory is probably far more common in nature than is suggested by current literature, but with recent species declines, many such dispersal systems might be lost before they can be identified.

comprise two or more steps involving the same mechanism (e.g. repeated caching of a nut by the same or different animal), because the change in the mode of seed dispersal in diplochory has important implications for the fate of seeds that are not inherent in simpler forms of multi-step dispersal. Diplochory is rapidly gaining recognition as a common means of seed dispersal in temperate and tropical communities, helping to clarify the selective forces acting

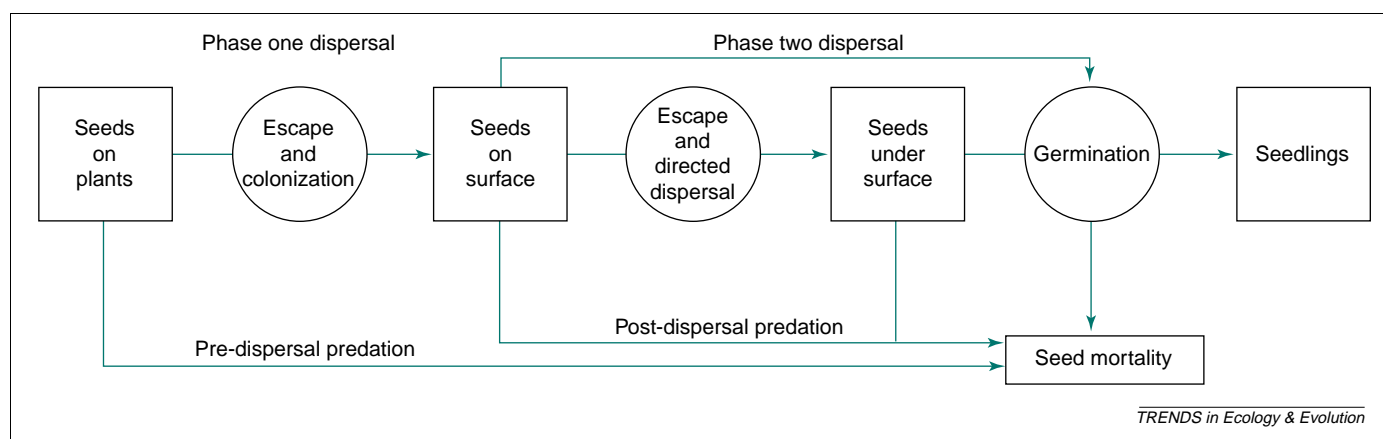


Figure 1. Potential benefits of diplochory, illustrating the main influences on seeds from the time that they are produced until they germinate and establish new plants. Rectangles represent physical states, arrows represent a change in state caused by dispersal, predation or germination, and circles represent the most important advantages resulting from dispersal.

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Glossary

Ballistic dispersal: abiotic dispersal by mechanical ejection of a seed from a fruit.

Diaspore: any propagative structure of a plant, especially one that is easily dispersed, such as a seed.

Elaiosome: a food body (usually rich in lipids or proteins) attached to the outside of a seed and attractive to ants.

Endozoochory: seed dispersal by vertebrates that ingest fruit and either regurgitate or defecate seeds unharmed.

Frugivore: any animal that eats fruit.

Myrmecochory: dispersal of seeds by ants.

Secondary dispersal: a second step in the dispersal of a seed after it first makes contact with a surface (i.e. primary dispersal). Phase Two dispersal is a special case of secondary dispersal, in which the second stage of dispersal is by a mechanism different from that of the first stage. Secondary dispersal is a more general phenomenon because primary and secondary dispersal can be by the same mechanism.

on plant reproduction and illustrating evolutionary trade-offs in the benefits of seed dispersal.

Howe and Smallwood [1] placed the potential benefits of seed dispersal into three categories: (i) escape from density-dependent or distance-responsive seed predators, pathogens or seedling competition near the parent plant [2]; (ii) colonization of suitable habitat at some relatively great distance from the parent plant [3,4]; and (iii) directed dispersal via some nonrandom process to specific sites that offer a disproportionately high probability of seedling establishment [5]. The ideal dispersal system maximizes all three benefits, but few, if any, single means of dispersal seem capable of doing so. For example, wind dispersal can provide escape and colonize new areas, but is ineffective at targeting specific sites because wind moves seeds at random with respect to establishment sites. Likewise, MYRMECOCHORY (see Glossary) can provide escape and target specific establishment sites [6], but is not very effective at colonizing new patches because ants do not carry seeds very far [7–9].

Here, we describe five seed dispersal syndromes that demonstrate diplochory and summarize the advantages and disadvantages of diplochory to plants. We also discuss the importance of diplochory in the evolution of seed dispersal and its implications for diversity and conservation in ecological communities.

Two-phase seed dispersal systems

Wind dispersal and scatter-hoarding animals

Animals scatter hoard the seeds of several plants that are initially dispersed by the wind, most notably pines (e.g. Jeffrey pine *Pinus jeffreyi*, sugar pine *P. lambertiana* and Coulter pine *P. coulteri*) of semi-arid forests of western North America. The cones of these pines open at maturity or after fire, and have seeds with a well developed wing that helps move seeds away from the parent plant. However, compared with pine seeds that are dispersed solely by wind, most of these pines have large seeds with heavy wing loadings [10], which makes wind a relatively ineffective means of primary dispersal. Most seeds land within one tree height of the parent tree, although a few can be dispersed many kilometers [3,4].

Pine seeds on the ground are vulnerable to animals that act exclusively as seed predators (e.g. bears, quail and

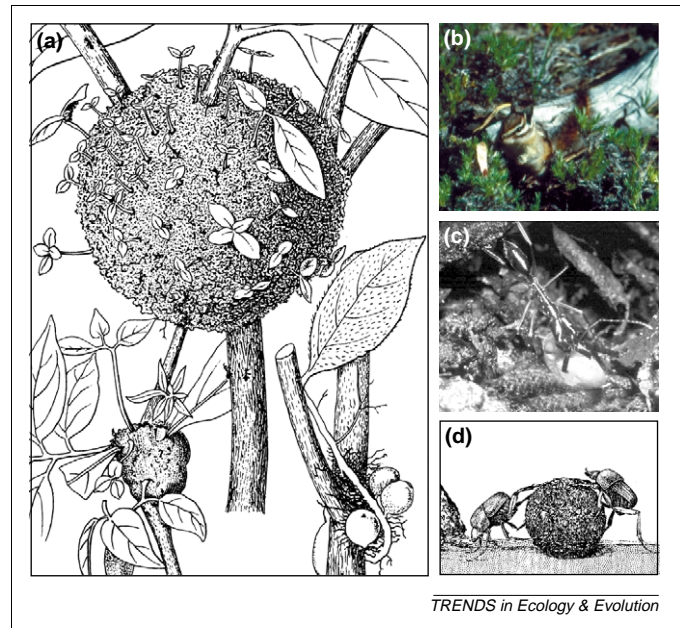


Figure 2. Examples of diplochory. (a) Epiphytic ant gardens at different stages of development. Many of the plants in these ant gardens are dispersed by the combined activities of frugivorous birds (phase one dispersers) and ants (phase two dispersers) ([30,31,56] reproduced with permission from [57]). (b) A yellow pine chipmunk *Tamias amoenus* about to grasp a winged Jeffrey pine *Pinus jeffreyi* seed. Chipmunks are very efficient foragers for wind-dispersed seeds and scatter hoard most seeds that they find in the soil often under shrubs, where they have a relatively high probability of establishing seedlings [12,58]. (c) An *Odontomachus chelifer* worker carrying a diaspore of *Clusia criuva*, which was initially dispersed by birds in their feces (photograph by Luciana Passos, reproduced with permission from Blackwell Publishing [9]). (d) Dung beetles rolling a dung ball. The beetles bury the dung with its seed contaminants and seedlings emerge if the burial depth is suitable (courtesy of CSIRO, Australia).

sparrows), but are also gathered by secondary dispersers (e.g. chipmunks, mice and jays), which eat some seeds but transport others to cache sites (Figure 2). Removal rates of simulated wind-dispersed pine seeds range from 10–90% d⁻¹ [11,12], and animals harvest most of the available seeds between seed fall and onset of winter (~2 months). Rodents usually cache seeds in the soil or plant litter 5–30 mm deep, and dispersal distances can exceed 100 m [13,14].

Although only a few of the cached seeds are eaten immediately, these scattered caches do not last long, because most stored seeds are removed within days or weeks [12,15]. Many recovered seeds are recached elsewhere, usually within 50 m of the original cache. Scatter-hoarded seeds are spatially dynamic, with many seeds residing in three or more cache sites during autumn. The number of cached seeds gradually declines as winter approaches, because of consumption by animals and because rodents transfer some seeds to their winter larders.

Ballistic dispersal and myrmecochory

Various plant taxa, from sclerophyllous shrubs and trees in the arid Mediterranean chaparral of Australia and South Africa to herbaceous annuals in mesic deciduous forests of eastern North America, disperse seeds short distances using explosive ejection or BALLISTIC DISPERSAL [16,17]. Seeds of many such plants are subsequently dispersed by ants, which is a common dispersal mechanism in these communities [16].

Seeds of plants that utilize ant dispersal often have an ELAIOSOME that is attractive to ants [18]. This typically comprises ~10–50% of total DIASPORE mass, although seeds dispersed ballistically usually have a relatively small elaiosome compared with species lacking ballistic dispersal [18]. After transporting seeds, ants consume the elaiosomes and either leave seeds buried intact in a nest chamber or place them in refuse piles outside the nest. Ballistic dispersal typically scatters seeds <5 m from the parent plant [18], and ants usually move seeds another 0.5–3.5 m [7,16,19]. Plant species with seeds secondarily dispersed by ants have shorter ballistic dispersal distances than do those that use only ballistic dispersal [20].

ENDOZOOCHORY and dung beetles

Herbivores and FRUGIVORES often consume plant material that is rich in seeds, and most fruit consumed by frugivores is adapted for this means of dispersal [1]. Seed residence times in animal guts range from minutes to weeks, and seed dispersal distances range from meters to kilometers. Many seeds dispersed via vertebrate guts are viable, although those deposited in feces can be destroyed by biotic and abiotic factors, including insects, fungi, rodents and desiccation [21].

Dung beetles (subfamily Scarabaeinae) are ubiquitous in warm temperate and tropical regions and play an important role in the removal of animal dung. They exhibit a range of dung acquisition and burying behaviors, from burying dung directly below the dung deposit to forming and then rolling dung balls 1–2 m to burial sites (Figure 2). The means of dung transport influences how quickly dung gets buried and the depth of dung and seed burial [22].

Rodents (e.g. spiny pocket mice *Lyomys* spp., New World mice *Peromyscus* spp. and spiny rats *Proechimys* spp.) play an important role by removing seeds from dung on the ground surface and from dung beetle nests [21,23–25]. Because dung beetles do not consume seeds, they do not compete directly with rodents, but rodents can interfere with the nesting and foraging behavior of the beetles by removing seeds from dung provisions [21,24]. Beetles can reduce this interference by sorting seeds out of dung provisions whilst preparing their nests. Dung beetles bury dung 1–80 cm or more deep, with most buried 1–10 cm deep [21,22,26,27]. Rodents often remove seeds when dung is buried within 2–3 cm of the soil surface. Seedling establishment is likely to occur in a narrow range of depths (~3–10 cm), where seed removal by rodents is low but seedlings can still emerge [21,24,26].

Endozoochory and scatter-hoarding rodents

Rodents actively gather seeds that are defecated or regurgitated by vertebrates. For example, spiny pocket mice *Liomys salvini* removed most guanacaste *Enterolobium cyclocarpum* seeds in a sample of horse dung in a single night [23]. Similarly, harvest of seeds by spiny rats, mice and agoutis *Dasyprocta punctata* is also rapid [21,22,25,28,29]. It is generally assumed that rodents eat most of the seeds that they take from feces or regurgitate, but the fate of removed seeds has, until recently, received little attention. Many of the rodents that remove seeds from feces are also avid scatter hoarders, and there is no

reason why they should be any less effective at dispersing defecated seeds than they are at dispersing seeds found in other situations.

The caching of large seeds from feces is a common process in tropical rain forests. Agoutis in Costa Rica scatter hoarded 27–46% of *Guarea glabra* seeds taken from feces [29]; in Panama, agoutis buried 56–66% of the *Virola nobilis* seeds that they took from simulated fecal deposits [28]; and spiny rats in French Guiana cached 16% of *Chrysophyllum lucentifolium* seeds taken from feces [25]. These rodents usually buried seeds within 5–15 m of the dung deposit [25,29], and cache sites were usually 1–3 cm deep in soil [29] or under plant litter [25]. Over one-third of cached seeds remained in place until the time of seed germination [25,29]. Although there are relatively few documented cases of this form of diplochory, we suspect that there is great, unrecognized potential for rodents to be secondary dispersers of seeds that they take from feces.

Endozoochory and myrmecochory

Diplochory involving frugivory followed by myrmecochory is widespread in tropical forests (Figure 2) [8,9,30–34], and probably more common than is currently realized in temperate habitats. Diaspores adapted for both these modes of dispersal generally offer two distinct food rewards: fruit pulp that is attractive to vertebrate frugivores and an elaiosome that passes through the digestive tract of the frugivore and attracts ants [31,33,35]. Ants carry seeds back to their nest and either store them or remove the food bodies and discard the seeds. For example, in southern Brazil, birds consumed 83% of the diaspores of *Clusia criuva*, a dominant rain forest tree, and ants then removed 98.5% of the diaspores from bird feces, taking most to nests and removing the lipid-rich elaiosome and discarding the seed in refuse dumps [9]. When an elaiosome is absent, seeds eliminated by frugivores are still attractive to some ants [34,36–38], and consumed seeds serve as rewards for the dispersal of other seeds, as occurs with scatter-hoarding vertebrates. This means of dispersal is probably successful because stored seeds get lost in nest galleries and many ant species move nest sites frequently, providing opportunities for neglected seeds to germinate [36].

Characteristics of phase one dispersal

Phase one dispersal in the examples considered here serves to lower density-dependent seed mortality near the parent plant. Explosive ejection of seeds scatters them, thereby reducing losses to seed predators that specialize on aggregated seeds [16]. Frugivores, herbivores and the wind scatter seeds and this avoids heavy seed predation by animals [13,21,24,39]. Seeds are not objects of interest in phase one of any of the five forms of diplochory described here. In all five cases, seeds are either dispersed by abiotic processes or by animals that digest something other than the seeds themselves (e.g. fruit pulp).

Most forms of phase one dispersal considered here can move seeds relatively long distances. Frugivores and herbivores can carry seeds many kilometers in their guts, and the wind has the potential to move some pine

seeds far beyond the limits of the local population. Only ballistic ejection of seeds is incapable of long range dispersal.

Phase one dispersal plays little or no roll in directing seeds to favorable establishment sites. In most of the cases considered here, phase one seed dispersal is random with regard to potential safe sites, although frugivores can sometimes move some seeds toward certain favorable habitats [40]. Furthermore, in all of the above mentioned examples, seeds are deposited on the soil surface, sometimes in dense aggregations (e.g. in a fecal deposit), where they are still vulnerable to seed predators, intense competition and desiccation.

The probability of seedling establishment at the end of phase one dispersal is relatively low. The exposed micro-site either does not stimulate germination or germination is subjected to a high rate of failure. If seeds germinate in a dung deposit or other type of aggregation, seedlings are likely to experience intense competition [31,33]. Some seeds are lost to seed predators, and the removal of seeds by agents of phase two dispersal diminishes the number of seeds available for germination [11].

Characteristics of phase two dispersal

Activities of phase two dispersers often serve to reduce seed predation. Animals that remove seeds from feces often bury them in soil or plant litter, where they are relatively safe from seed predators [28,29]. Rapid removal of pine seeds from the forest floor by seed-caching rodents reduces seed predation by non-seed-caching species. Deposition of seeds in nests or refuse piles by ants reduces losses to aboveground seed predators [16,32]. Ants can also reduce fungal attack on seeds by cleaning them of perishable fruit pulp or fecal material [32,37].

The services of phase two dispersers often come with a cost in the form of seed embryos that are consumed. Seed-caching rodents and birds only cache seeds so that they can eat them later. This mode of seed dispersal is effective because the scatter-hoarding animals cannot relocate all stored seeds [14]. Ants and dung beetles can bury seeds too deeply to enable seedlings to emerge, and some ant species also consume the seed [21,34,41].

Phase two seed dispersal seldom offers any great advantage in terms of increasing dispersal distance. Most modes of phase two dispersal increase total dispersal distance by only a few percent. For, example, dung beetles and ants move seeds only a few meters. Rodents usually carry seeds from frugivore and herbivore feces <5 m [25,29], but chipmunks typically carry wind-dispersed pine seeds 10–60 m to cache sites [12,13]. SECONDARY DISPERSAL by ants can double that achieved by ballistic dispersal [16,19,42,43], but the total dispersal distances are so short that it seems unlikely that the benefits of secondary dispersal lie in increased dispersal distance. More important than dispersal distance *per se* is that phase two dispersers scatter seeds around the site of phase one deposition, and therefore reduce the likelihood of seed predation.

Perhaps the greatest advantage of phase two dispersal is that animals move the seeds to situations that are more favorable for seedling establishment. Ant nests and refuse

piles can provide ideal microsites for germination and seedling establishment. In some cases, these sites offer nutrient-rich substrates (high levels of nitrogen and phosphorus) for seedlings [30,42,44], which can be essential to survival because many myrmecochores occur on nutrient-poor soils [45,46]. The more aerated soils found around ant nests also benefit seedlings because of their greater moisture-holding capacity. In fire-prone environments, burial of seeds can provide a safe site from intense heat [41,47]. Dung beetles bury many seeds within the range of depths that are favorable for seedling establishment [21,22,24,26,27] and deposit seeds among quantities of organic fertilizer, which increases seedling growth rates. Rapid burial of dung prevents the dung and seeds from drying out, which helps maintain seed viability and favors seedling establishment. The behavior of seed-caching rodents is often directed (coincidentally) toward forest openings, where the probability of seedling establishment is greater [13,29]. Caching by rodents places most seeds in a substrate and at a depth that is suitable for seedling establishment. Scatter-hoarding animals represent an effective means of seed burial, which can be a crucial process for large seeds that is difficult to achieve by other means.

Most importantly, phase two dispersal increases seedling establishment and survival above that achieved by phase one dispersal. As much as 14% of the Jeffrey pine seeds cached by chipmunks remain viable in intact caches in spring [12,15], but it is uncommon for seedlings to result from seeds dispersed solely by the wind because animals eat or cache > 99% of them [11]. Seeds taken from feces and buried by rodents are more likely to result in seedling establishment than are those left in feces or on the ground surface [28,29]. Removal of seeds from feces by ants increases germination rates [9], and increased rates of seedling establishment have been demonstrated for seeds of plants that are deposited in ant refuse piles [6,9,19,34,44]. Seeds buried by dung beetles are also safer from predators and are more likely to establish seedlings than are those left in dung deposits [26,48]. By scattering seeds in feces, phase two dispersers often act to reduce seedling competition [25,33,49,50].

Evolution and adaptive significance of diplochory

Have these forms of diplochory evolved or are they accidental combinations of seed dispersal mechanisms? Considered singly, two forms of seed dispersal acting sequentially might seem like a haphazard pairing of two seed dispersal agents. But when considered as a collection, where different forms of diplochory have similar effects on plant fitness and where individual examples within a particular type of diplochory share common characteristics even though the taxa involved are not related, a non-adaptive explanation for diplochory seems unlikely. Forms of diplochory might arise and persist because they are adaptive, and, once configured, diplochory can evolve as the plants evolve traits that facilitate two different forms of seed dispersal simultaneously. If a new second phase of dispersal is added to an existing form of primary dispersal, then selection might favor the acquisition of new traits that serve to attract phase two dispersers. The existence of

Box 2. Future research

- More detailed understanding of seed fates. The study of secondary seed dispersal, and more specifically diplochory, has been slow to emerge because it is difficult to follow the fates of large numbers of individual seeds through even one dispersal phase. Those interested in seed fates must be tenacious at tracking seeds beyond primary dispersal to their ultimate demise or germination. Fortunately, several tools have been developed to track seeds, including seed tags and radioisotopes [13,25,28,29].
- Better knowledge of complex seed dispersal systems. The five forms of diplochory described here are still poorly understood, and there are other forms for which there was too little information to include, and still others that probably have yet to be discovered and characterized. Before we can fully understand the importance of diplochory, we need more information about its geographical and ecological distribution, the types of environment that promote its development, its prevalence relative to other forms of seed dispersal, and the plant taxa that are dispersed in this way.
- Partitioning seed mortality and plant fitness. To understand thoroughly the benefits of seed dispersal, we need a better understanding of where mortality occurs along complicated, multi-phase seed fate pathways. For example, what proportion of seed mortality occurs as part of phase one dispersal versus phase two dispersal and what are the causes of seed mortality during each phase? What happens to seeds in the absence of removal by phase two dispersers? What is the likelihood of seedling establishment with and without the action of secondary dispersal? How do changes in seed microsite affect the probability of seedling establishment? Ideally, it would be desirable to partition the contribution of different phases of dispersal to plant fitness.
- Measuring the benefits of dispersal. Currently, it is difficult to compare the relative contributions that a particular agent of dispersal makes to plant fitness. Such an objective measure seems well within our grasp, using the number of seeds as the currency and the proportion of the seeds of a plant that survive and reach a site that permits establishment as the dependent variable. The difficult part is to decide about the appropriate criteria that define colonization and directed dispersal and to follow accurately a large enough population of seeds to estimate those parameters.
- Phylogeny of diplochory. Little is known about the phylogenetic history of diplochory. A phylogeny of diplochorous plant species and their nondiplochorous relatives that is correlated with phenotypic traits important in seed dispersal could be very revealing. For example, in plants that are dispersed ballistically followed by myrmecochory, which evolved first, the ballistic mechanism or elaiosome? A phylogenetic analysis would help reveal which traits are derived and the sequential pattern of evolution.

these traits might reduce or alter the original effectiveness of phase one dispersal. For winged pine seeds secondarily dispersed by seed-caching rodents, for example, rodents select for larger seeds and, indirectly, larger cones and longer wings on seeds [39]. However, because of aerodynamic considerations, these heavy seeds are not likely to be carried very far by the wind, diminishing the effectiveness of phase one dispersal [10]. In other cases, the acquisition of a new second phase of dispersal might have some subtle effects on seeds, but have no effect on the effectiveness of the original disperser, which is probably the case with seeds in the feces of vertebrates dispersed by dung beetles.

Diplochory generally involves multiple species of phase one and phase two dispersers, and the same sets of dispersers can effectively disperse the seeds of multiple plant species. Although the species-specific interactions that accrue a net benefit to plant fitness are usually unclear, many beneficial associations do occur. This has led to the characterization of seed dispersal in general, and of diplochory as a specific example, as diffuse mutualisms [5,9]. Perhaps the main argument against the view that diplochory benefits all interacting species comes from questions about the likelihood or frequency of directed dispersal in nature [5,51], which we suggest is the primary benefit offered to plants by phase two dispersers. However, Wenny [5] has recently provided detailed arguments and supporting examples suggesting that directed dispersal is far more common than was previously assumed.

Implications for conservation

Numerous species often interact in complex seed dispersal systems, and diversity might also be an outcome of community interactions in these systems. A recent study demonstrates that escape of seeds from seed predators near parent plants, which we attribute to both phase one and phase two dispersers, maintains tree seedling diversity in a tropical forest [51,52]. This provides

empirical support for a long-held theoretical prediction and a powerful argument for the conservation of seed dispersers. There are also good reasons to be concerned about the maintenance of seed dispersal systems. For example, forest fragmentation in central Amazonia has pervasive effects on the assemblage of dung beetles that act as phase two dispersers, and large beetles (the only ones able to move some large seeds) were disproportionately vulnerable to extinction in small forest fragments [48]. The density of seed predators also increased in fragments [48]. In central Amazonia, forest fragmentation changed the species composition of litter-dwelling ants, and there were fewer ant species and reduced nest densities in fragments relative to continuous forest [53]. In southern California, native harvester ants *Pogonomyrmex* spp. that secondarily disperse ballistically ejected seeds of the tree poppy *Dendromecon rigida* considerable distances are rapidly being replaced by invasive Argentine ants *Linepithema humile* that move the seeds only a few centimeters [38]. Argentine ants have also displaced native seed-dispersing ants in South African shrublands, resulting in dramatic changes in plant community composition, in which the density of large seeded plants is disproportionately decreased [54]. In Uganda, humans derive resources from 42% of 77 tree species for which frugivorous primate species, which are increasingly threatened by hunting and habitat loss, constitute important phase one dispersers [55].

Considering the current accelerated rate of species declines and the complexity of diffuse interactions involved, many diplochorous dispersal systems might be compromised or lost before they are recognized. We must achieve a deeper understanding of complex seed dispersal systems (Box 2) to help us better comprehend the selective forces acting on fruit and seed characteristics, understand plant–animal interactions, and conserve these interesting and ecologically important relationships.

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